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On Natural Selection and Separation.

By Arnold E. Ortmann.

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I. It is generally understood that the chief merit of Darwin in creating his theory of the origin of species is the establishment of the principle of Natural Selection, and that by the introduction of this principle the process of development of organic nature from the conditions existing in former times to the present may be made intelligible, and mostly it is also understood, that natural selection is only one of the factors playing a part in the formation of species. But the proper line of action of natural selection, as conceived by Darwin, is estimated by some other authors very differently. I refer especially to Weismann, who calls natural selection "all-sufficient," which implies that it is the only factor that forms species; but I regard this expression only an exaggeration, since Weismann contradicts himself in this respect.* The assertion, however, stands, that natural selection of itself *may* form different species. On the other hand, Eimer maintains, in opposition to Weismann, that there is

* See Ortmann, *Grundzüge der marinen Tiergeographie*, 1896, p. 30.

no formation of species by natural selection, but that the only action of this factor consists in the preserving of existing species.* This opinion is as erroneous as that of Weismann, but in the opposite direction.

So far, however, Darwin's definition of natural selection, as the survival of the fittest, was not altered, only the efficacy was regarded differently. But recently Pfeffer† has given another conception of natural selection, differing from Darwin's. According to the latter, by the struggle for existence the fittest are selected (hence the term "selection"), while all others are destroyed. Pfeffer, however, says that there is no selection of particularly good variations, but the struggle for existence destroys indiscriminately fitted and not fitted individuals, and certainly it destroys all the not fitted. Thus the surviving remainder (according to Darwin's terminology the selected part) consists of a number of good and better individuals, which show a *good average*. The struggle for existence continued in this way during many generations—destroying all the bad individuals—effects little by little that this good average improves from generation to generation. Pfeffer calls this process "Transformation of species by self-regulation" ("Umwandlung der Arten durch Selbststeuerung").

This conception of natural selection differs only slightly from that of Darwin, and one could say, that only the form of expression is different, while the effect in both cases is the same. But we shall see below, that the form used by Darwin is in some respect inferior to that used by Pfeffer, and although Darwin's meaning is nearly the same as that of Pfeffer, we shall have some advantage in accepting Pfeffer's phrase, especially in maintaining, that not the fittest, but good individuals survive, and that the change effected is an extremely slow one.

Recently I have pointed out,‡ that this "transformation of species" is nothing else than the well-known "mutation" of palæontologists, a term, the differences of which from "variation" are first shown by Waagen and Neumayr, and subsequently most vigorously maintained by W. B. Scott.§ These differences are neglected by many zoölogists, although the "comparatively lawless and uncontrolled character"‖ of the variations and the "directness of advance towards the final goal"¶ of the mutations differ strikingly. Scott says:** "While variations are due to the union of changing hereditary tendencies, mutations are the effect of dynamical agencies acting long in a uniform way and the results

* Eimer (*Die Artbildung und Verwandtschaft bei Schmetterlingen*, ii, 1895, p. 33) uses even the expression: "Inefficiency of Natural Selection" ("Ohnmacht der Naturzüchtung")

† Pfeffer, "Die Umwandlung der Arten, ein Vorgang functioneller Selbstgestaltung," *Verhandl. Naturw. Ver. Hamburg* (3) i, 1894.

‡ *Grundzüge der marinen Tiergeographie*, p. 31.

§ Scott, "On Variations and Mutations," *Amer. Jour. Sci.*, 48, 1894, pp. 355–374.

‖ *l. c.*, p. 370.

¶ *l. c.*, p. 360.

** This sentence is first given in the paper "On the Osteology of Mesohippus and Leptomerys," *Journ. Morphol.*, v, 1891, p. 388, and repeated *l. c.*, p. 372.

controlled by natural selection." If thus mutation is influenced by natural selection, it implies, that any particular mutation must advance in a direction advantageous for the respective species, and, indeed, many examples of mutation known among fossil animals are apparently due to the advantage produced by the change.* I must add here, however that probably not all mutations (in a palæontological meaning) are due to natural selection, but that many do not imply an actual improvement. In this respect Eimer's investigations of the Papilionidæ are important. The variations in the colors of the wings, on which Eimer exclusively relies, are apparently neither useful nor injurious, yet they are caused most likely by external conditions, for example, by warmth or cold during the development of the imago from the larva. Eimer points out, that in his butterflies a distinct direction of variation is evident, which he calls "Orthogenesis." We shall see below that this is a process of inheritance. By the constant action of certain external causes upon subsequent generations, and the repeated inheritance of the characters thus acquired, a certain tendency of variation in a distinct direction may develop. If this tendency does not bear on utility, the degree of variation in the single individuals differs considerably, and even individuals varying in other directions are preserved. Thus a gradual transition results from the less to the more changed individuals. But altogether, from generation to generation, the variation in that direction increases, and the changed individuals may become the most numerous, thus effecting a slow change of the average characters of the species, which looks exactly like a mutation. We may call this latter mutation, produced by accumulative inheritance, by Eimer's term "orthogenesis," in contrast to the "mutation" produced by natural selection. "Orthogenetic mutations" are also known among fossil animals, and I refer† especially to the group of Ammonites whose mutations have been first studied. Here most of the characters advancing in certain lines, ornaments and form of the shell, etc., are apparently not subject to natural selection. Of course, we do not know, in most of the cases, whether a particular transformation is useful or not, and in many cases, where we cannot recognize any advantage, the latter is present nevertheless. But since Eimer's investigations have amply proved that such changes, indifferent as regards utility, are certainly present in living animals, they must also have been present in fossil animals.‡

*I mention only the example of the transformation of the structure of the extremities in the horse-phylum, as discussed by Scott (*l. c.*, p. 368). With the change of one character in a useful direction the change of others may be connected, which are in correlation with the first. This would be an indirect action of natural selection."

†A very illustrative example of "Orthogenesis" is the transformation of the Miocene and Pliocene *Fulgur contrarius* into the Pliocene and Recent *Fulgur perversus*. See Leidy, "Remarks on the Nature of Organic Species," *Trans. Wagner Free Inst. Sci.*, ii, 1889, p. 51ff., Pls. 9 and 10.

‡Weismann indeed denies, even in respect to Eimer's butterflies, that there are any useless variations, but this is one of his many assertions, which he does not even try to establish properly (comp. "Germinal Selection," *The Monist*, Vol. 6, No. 2, Jan., 1896,

We cannot say, however, that animals subject to orthogenesis are not at all under the influence of natural selection: the latter must necessarily act also upon them, since all injurious variations are destroyed and cannot be transmitted and give cause to orthogenetic mutations. Natural selection does not invariably imply mutation, but often, especially if the external conditions are unchanged, it effects only a *preservation* of an existing species: by destroying all bad individuals it maintains the good standard of the characters of the survivors, and only if there is any advantage in any variation, this standard will be improved in a direction indicated by this advantage. Thus we may say that natural selection gives origin to mutation in a useful direction, but that this mutation is very slow, and often so infinitesimal, that it amounts almost to nothing, that is to say, only the good standard is saved. This action of natural selection effects besides the general adaptation of each animal form: the surviving individuals comply with the requirements of the surrounding conditions of life.

We have no reason to look upon natural selection as a factor of minor importance, as Eimer is inclined to do. Even the preserving of a good standard is all-important. Natural selection is a factor which cannot be left aside, and which is a necessary one in the development of all beings, and it is a grave mistake to abate its value in favor of any other factor coöperating in the formation of species.

II. Yet the value of natural selection has not only been underrated by some authors, but, on the contrary, it has been overrated, especially by Weissman. The latter believes that natural selection does form species. One can hardly understand on what grounds he is induced to allege this action, and why he even believes that it is the only factor in the formation of species, since he himself accepts Darwin's conception of this factor, namely, that it acts selectively upon the best variations, and destructively upon all the others, thus inducing only a change, a transformation of *one* existing form or species into *one* other, but never causing the origin of *divergent* forms or species. This point is so plain, and so beyond any doubt, that only a great logical mistake, and a complete misapprehension of Darwin's theory on the part of Weismann can explain this error. Yet it is perhaps a little difficult, to say precisely, where the fallacy is hidden, and it would be interesting to examine this point more closely.

I have no doubt that this wrong interpretation of natural selection is

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p. 254). Weismann's argument as respects this point is the following: Eimer believes to have shown, that there are no advantages for the respective species visible in the different colors of the butterflies: but since I (Weismann) have propounded the theory, that all characters are due to natural selection, the latter must have produced these color markings also, and we must *assume*, that they are or were nevertheless advantageous! Comp. Spencer (*The Inadequacy of Natural Selection*, 1893, p. 49): "He (Weismann) practically says: Propound your hypothesis; compare it with the facts; and if the facts do not agree with it, then assume potential fulfillment, where you see no actual fulfillment."

due to the form in which Darwin has given the definition of this term. I am confirmed in this belief, as the same error is committed again and again. Still very recently, at the last meeting of the German Zoölogical Society, in the discussion following Eimer's discourse, Ziegler* expressed his opinion that no important difference exists between Darwin's natural selection and Pfeffer's; that it is irrelevant whether one says that the fittest is selected, or that the not fitted are destroyed: both processes have the same or nearly the same result, as may be at once understood by an example he quotes from the breeding of races in domesticated animals.

But even this reference to man's selection in domesticated animals, and the unconditional comparison of it with natural selection, is the weak point, and apparently the term "selection" used by Darwin† induced this error. I shall demonstrate here, that both processes, the natural and the artificial, are certainly not identical, although apparently similar, and especially that the final results of both are entirely different. It is true, Darwin himself avoided this mistake,‡ but it was certainly made by subsequent authors, and especially Weismann must have fallen into it, since his odd misinterpretation of natural selection could otherwise hardly be intelligible.

Weismann apparently has reasoned in the following manner. Natural selection effects that individuals possessing certain useful characters are preserved in the struggle for existence, and man's selection in domesticated animals has a similar effect, preserving individuals provided with certain characters desired by the breeder. Consequently both processes are completely identical, with the only modification, that in the first the principle of utility is ruling, in the second the wishes of man. Farther, since in domesticated animals a great number of varieties or races are often obtained from a single original species, and since these races do not differ in their morphological differentiation from natural species, and indeed are perfectly analogous to the latter as regards their relation to the ancestral forms, it was believed that the natural species originated exactly in the same manner, that is to say, since under domestication different races are obtained by man's selection, in nature different species are formed by natural selection. By this argument, I believe, Weismann came to the view, that species are formed by natural selection alone, and although this opinion of the complete parallelism of natural and man's selection is nowhere explicitly given in his writings, we have to infer it.§

*See *Verhandl. deutsch. Zoolog. Gesellsch.*, 1895, p. 129.

†Darwin, *Origin of Species*, 6th ed., 1878, p. 49: "I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection, in order to mark its relation to man's power of selection." Comp. also p. 65, *ibid.*

‡It is well to be noted that Darwin did not commit this mistake, and that he always regarded natural selection only as taking part in the formation of species, but not as the only cause of it. This is already amply demonstrated by Romanes ("The Darwinism of Darwin and the Post-Darwinian Schools," *The Monist*, Vol. 6, No. 1, October, 1895, p. 3ff.).

§I do not know whether I have succeeded in trying to follow Weismann's thoughts, but I confess freely: if he did not reason as I have conjectured above, I am at a loss to understand him at all on this point. But if the latter is the case, I do not think it is a fault of mine.

But if we analyze the action of man in breeding, we shall find that it does not correspond to natural selection, but is more complex, and that accordingly the final result obtained by man is different from that in nature.

The breeder selects from a certain species a number of individuals fitted for his particular intentions. The whole number of individuals of this species is thus divided into two parts : the *selected* and the *rejected*. By natural selection also the individuals of a species are divided into two parts: the *fitted* and the *unfitted*. There seems to be complete analogy, but this is not the case. In natural selection, as we have seen above, the fitted survive, and the unfitted are destroyed. But in man's selection there is a difference: of course, the selected corresponding to the fitted survive, but the rejected corrresponding to the unfitted are not invariably destroyed. On the contrary, they survive too, at least a great number of them. It is not at all in the breeder's power to kill all the individuals not wanted of the species under domestication ; he may kill of a particular litter, perhaps of all his stock those not corresponding to his wishes, he may continue this killing during a series of generations, but he never can succeed in destroying all the rejected individuals of the original species with which he deals. On the contrary, this original species will propagate, and will continue to exist beside the new race obtained from it. The result of the breeder's art is a new race coëxisting with the original species.

See the difference. Natural selection preserves only a number of individuals possessing a certain number of useful characters, while all the others are destroyed: it preserves the good standard of the species or may even improve it. Man's selection, however, gives origin to a new race branching off from the original species, which is preserved, too, and may be subject for itself to the action of natural selection or may be domesticated and subject to breeding again. Therefore, it is easily understood, that it is certainly incorrect to look upon natural selection and the art of the breeder as analogous processes, and natural selection cannot be the cause of the origin of different species.

We may, however, safely say that the races obtained by the breeder are analogous to natural species, and we are to examine by what additional factors the complete parallelism of the breeding of races and the formation of different species in nature is accomplished.

Recently* I have endeavored to demonstrate that we are to imagine natural selection supplemented by the process of *Separation* (or *Isolation*), in order to understand the development of coëxisting different species from one original species. The main point in separation is the action of different conditions of life in different localities separated from each other. The descendants of one ancestral form, if separated *under different conditions*, tend to develop separately, and the directions of either mutation or orthogenesis become different in each separated group : another

* *Grundzüge der marinen Tiergeographie*, pp. 31, 32.

average fitted for the particular conditions of life, or another direction of orthogenesis prevails among the surviving individuals of each group, and after a *permanent* separation during a series of generations the changes in each separated group amount to what is called specific differences.

If we compare in this respect the origin of species in nature with the art of the breeder, we see at once that separation is implied in the action of man. The breeder not only selects his material—in so far he complies with the requirement of natural selection—but he isolates it from the other individuals, and farther on, his chief occupation is the repeated application of the same principle in the separated stock of animals and their descendants, namely, the selection only of individuals answering his wishes. This action corresponds exactly to natural selection in isolated localities. Thus the breeder clearly unites two different actions. (1) The selection of particular individuals possessing certain desired characters corresponds to natural selection. But the breeder cannot, or cannot completely, destroy the rejected remainder. (2) Accordingly he directs his chief attention to the isolation of the selected material, in order to secure control over the true breeding in subsequent generations. Since the organisms kept under domestication are mostly amphimixotic,* the breeder must exclude especially the possibility of interbreeding with the outsiders. This latter point, although clearly understood by Darwin† himself, has been overlooked generally. It was forgotten, that beside the material used for breeding, there exists other "raw" material, and that the preservation of the latter constitutes a very important difference from

* As regards the origin of races as well as of species it matters nothing, whether the respective organism is amphimixotic or not (see *Grundzüge*, etc., p. 32). Amphimixis, that is to say propagation by crossing effects equality, the fusion of different characters, and *not*, as Weismann asserts, the appearance of new variations. This law is not only logically evident, but is amply demonstrated by facts. Comp. Darwin, *Variation of Animals and Plants under Domestication*, 2d ed., ii, 1876, p. 62ff., where numerous examples of the equalizing power of crossing are recorded. This question is to be looked upon as finally settled already by Darwin and no doubt in the most convincing manner, namely, by well-established facts. It is extremely unintelligible how Weismann could throw aside all the proofs carefully collected by Darwin and substitute his own ill-founded conception of Amphimixis. I may add here that between the action of Amphimixis and that of Panmixia as accepted by Weismann, there exists a grave logical error. Amphimixis is the simple process of crossing occurring but once, Panmixia is the same process repeated often and in different directions: the effects of both can only differ in quantity. According to Weismann, however, Amphimix of different animals results in new differences, Panmixia of different animals in the disappearance of existing differences (variations without value for selection are absorbed). This remains an insurmountable contradiction until Weismann demonstrates that his Amphimixis and Panmixia are conceptions contradictory to each other. Eimer (*Entstehung der Arten*, i, 1888, p. 48) says, Amphimixis may produce new things by uniting different things. That is true in so far as the offspring is different from either parent. But this is the first step in uniting the characters of the parents. *The single individuals resulting from the same or similar crossings are more alike to each other than the parents were to each other.*

† Darwin (*Variation under Domestic.*, ii, p. 62) says: "The prevention of free crossing, and the intentional matching of individual animals, are the cornerstones of the breeder's art," and "No man in his senses would expect to improve or modify a breed . . . unless he separated his animals."

the process of natural selection, where such a remnant corresponding to the "raw" material does not survive—unless a *separation* by natural conditions is added.

III. The principle of *Separation* or *Isolation*, first conceived by M. Wagner, is considered by nearly all authors* as a factor of minor importance, although nearly all have conceded, that its occasional action cannot be denied. It was looked upon as an additional factor now and then favoring the formation of species, but not as a necessary one. In the original theory of Darwin isolation is not contained as a particular factor, although Darwin recognized the value of it very well, but he understood it in a purely geographical sense.† As regards the formation of different species he believes‡ it to be explained by the *principle of divergence:* divergence is useful, and if there are any divergent variations within one species, he says (p. 87): "They will be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers." The introduction of this principle, however, is a mere circumlocution of "differentiation of species," not an explanation: we want to know, what are the *causes* of the divergence? If we peruse Darwin's writings in this respect, we find that he was very near to recognizing that separation actually effects the divergence,§ but since he understood separation only in a strictly geographical sense, he failed to put this factor in its proper place. Darwin's principle of divergence is nothing else than the result of separation, and if we substitute the latter for the former we shall complete Darwin's theory in a very important point.

Even Wagner, in introducing the principle of separation, did not give it its correct place within Darwin's theory, but tried on the contrary to replace, at least partly, selection by separation, and farther, he conceived the latter almost entirely in a purely geographical sense. Besides, he laid much stress upon the prevention of the crossing of the separated groups of animals, which is not at all the chief peculiarity of the action of separation. So have all other authors‖ in discussing this principle. But as we have seen, separation acts chiefly in the line, *that each separated group is subject to different conditions of life, and that thus the variations, the directions of inheritance and natural selection become different.* It does not act, however, always in this manner, since separation is possible

* I am to mention that G. Baur is almost the only author who estimates correctly the value of this principle. See the references to his papers: *Grundzüge*, etc., p. 29, footnote, and *Science*, March 6, 1896, p. 361.

† *Origin of Species*, Chaps. xii and xiii.

‡ *Ibid.*, p. 86ff.

§ Darwin (*Origin of Species*, pp. 98–100) uses even the words "confined or peculiar stations," and "isolated stations." On p. 169 he answers the question: "How . . . . can a variety live side by side with the parent species?" by the following: "If both have become fitted for slightly different habits of life or conditions, they might live together" and "the more permanent varieties are generally found, as far as I can discover, inhabiting distinct stations."

‖ For example, Haeckel and Weismann: see *Grundzüge*, etc., p. 31, footnote.

without a change or differentiation of external conditions of life: then a differentiation of species does not result, but we shall have the same species in separated localities. We call such species "relicts" from a former continuous distribution.*

Eimer, although he appreciates the value of geographical separation, names other causes besides: but what he calls "genepistasis" and "kyesamechania" are nothing else than particular actions of separation.

But for a plain understanding we should examine Eimer's theories more closely.†

Eimer‡ defends the opinion that variations are caused by external conditions, but that variability is not an indefinite one, but that the variations are comparatively few, and take place only in distinct directions. There is, according to him, no "fortuitous" or "irregular" variability, but a variability in certain few and distinct lines: he calls this the principle of *Orthogenesis*, and believes that it is contrary to Darwin's alleged supposition of unlimited and "fortuitous" variability. I can hardly see that this difference from Darwin exists at all. It is true Darwin uses the words "indefinite variability," but certainly not in the sense as interpreted by Eimer ("zufällig," "regellos"). Darwin says:§ "All such changes of structure, whether extremely slight or strongly marked, which appear amongst many individuals living together, may be considered as the indefinite effects of the conditions of life on each individual organism, in nearly the same manner as a chill affects different men in an indefinite manner, according to their state of body constitution," etc. That is certainly not a variability subject to casuality, but a variability governed by external causes, which may differ only according to the disposition of the individuals, and this opinion, that "the nature of the organism and the nature of the conditions"‖ are connected in the formation of variations, is also upheld by Eimer.¶

Further, he lays much stress upon the fact that variability advances in a definite direction (orthogenesis), but, I think, he confounds here two actions, that of variation and that of inheritance. Orthogenesis is variation, which is transmitted, and which is accumulated by the repeated action of the *same* external causes upon a series of descendants. We can hardly decide, whether a variation tends to advance in a distinct direction, unless we see that again and again specimens vary in the same direction,

**Grundzüge*, etc., p. 34 and p. 86.

†I go more into details here than seems perhaps necessary, because I consider Eimer's investigations as very important, especially as regards the facts collected. But we shall see that Eimer's views do not differ considerably from Darwin's, and that the chief differences are only differences of terminology.

‡Eimer, *Die Entstehung der Arten auf Grund von Vererbung erworbener Eigenschaften nach den Gesetzen organischen Wachsens*, i, 1888.

§ *Origin of Species*, p. 6.

‖ *Ibid.*, p. 6.

¶ Comp. *l. c.*, p. 5. Variation is effected by "Wechselwirkung zwischen der stofflichen Zusammensetzung des Körpers und äusseren Einflüssen."

and if we see the same variation present in different degrees in a large number of individuals, we have reason to suppose that inheritance plays a part, since the amount of change, if often inherited, must on the one hand increase, and since, on the other hand, the force of inheritance is generally different in each individual. Thus orthogenesis, variation in a distinct direction, is the result of the combined action of variation and inheritance: but it is perhaps advantageous to accept Eimer's term, because, as we have seen above, it is important as regards the transformation of species.

Orthogenesis results in series of variations consisting each of a number of individuals varying in the same direction but in a different degree: it unites the single variations into *varieties*, that is to say, into groups of animals showing the same tendency of variation. This grouping of variations into varieties is especially due to inheritance.

Eimer tries farther to find out the causes of the breaking up of any series of variations into *species*, and reaches the conclusion that species are formed when a certain group of individuals within a series "loses its connection with its other allies."* This breaking up of a series of variations in consequence of lost connection he calls "*genepistasis.*"† Under this head come, according to him, *Geographical Separation*, *Halmatogenesis*, and *Kyesamechania.*‡

If we direct our attention to the general definition of "*genepistasis*" given by him, that it is the losing of connection of certain groups, we see at once that genepistasis is exactly the same as separation, and under the same head comes *kyesamechania.*§ The latter term means that a sexual crossing between animals of more or less different characters is rendered impossible by morphological or physiological causes. This impossibility of crossing is certainly not the first *cause* of difference, but it is the *result* of already existing differences produced by beginning separation, and as respects the formation of species, kyesamechania can never be a primary cause of the origin of different species, but it is the result of the beginning differentiation, and may develop an additional factor accelerating the process of specific differentiation.

As regards *Halmatogenesis*, which means the sudden appearance of any new variation, Eimer explains this process by correlation:‖ but this explanation is insufficient. If any character changes, other characters connected by correlation with it change also, but if the change of the first is slow, certainly the changes of the others are so also, and a sudden change of characters by correlation presumes a sudden change of the leading character. Thus correlation cannot explain halmatogenesis.

* See *l. c.*, p. 26: "Wenn . . . . eine Gruppe von Individuen . . . . auf irgend eine Weise die Verbindung mit den übrigen Verwandten verloren hat . . . . spricht man von Arten."

† See *l. c.*, p. 30ff.

‡ I cannot make out with certainty what Eimer thinks as to the logical relations of these terms to each other, but I hope I have quoted him correctly.

§ See Eimer, *Die Artbildung und Verwandtschaft bei den Schmetterlingen*, ii, 1895, p. 14ff.

‖ See *Entstehung*, etc., p. 53.

But we do not need this at all. Halmatogenesis is a well-known process of inheritance, and comes under different heads in that chapter. For example, accumulative inheritance (even orthogenesis) may effect a sudden rise of the degree of development of a certain character, or characters remaining latent during one or more generations may come suddenly into reappearance, or farther, atavism may effect the same. Halmatogenesis does not at all play a part in the breaking up of a "chain of organisms," but it takes part only in the formation of varieties.

Therefore, of Eimer's new terms, only *Genepistasis* and *Kyesamechania* may form different species, and both are nothing else than *Separation*, or as Eimer himself says: "the interruption of connection."

By this brief sketch of Eimer's views we see that there is no considerable difference from Darwin's theory,* except that he considers natural selection to be of minor importance. This is probably due to the fact that he has investigated chiefly characters not at all subject to natural selection. He forgets, however, that even upon animals provided with indifferent characters natural selection must necessarily act in order to maintain the good standard of all the other characters. All the principles introduced by Eimer: Orthogenesis and halmatogenesis as forming varieties in a distinct direction, genepistasis and kyesamechania as forming species, are only new words for old ideas, which indeed have been set forth already by Darwin. And farther, these new terms are mostly results of well-known laws and not the primary causes of the formation of varieties or species, and they do not give us a better knowledge than before of the respective processes, in some cases, indeed, they may even induce confusion.

As respects *separation* we have seen that Eimer considers it only as an additional† factor causing specific differentiation, but farther we have seen that his genepistasis is also separation. Like all the other authors he apparently has conceived separation only in a purely geographical sense. I have, however, demonstrated‡ that we are to conceive the term *separation* in a *bionomical* sense, that is to say, that any causes "effecting a permanent interruption of the bionomical continuity between certain groups come under the head of separation. Separation keeps particular groups permanently under particular conditions, and thus they are prevented from migrating from one station of definite conditions of life into others with other conditions."

* Eimer identifies Darwin's theory with the "Darwinism after Darwin" (comp. *Artbildung und Verwandtschaft bei Schmetterlingen*, ii, 1895, Preface, p. v), in supposing that Darwin's theory alleges that species are formed by natural selection. But we know that this is an entirely unwarranted imputation.

† See *Artbildung*, etc., 1895, p. 9. I should like here to point out an apparent error in Eimer's arguments for the origin of new species in the middle of the range of the original form: he says (*ibid.*, p. 11) that the group of *Papilio asterias* originated from amidst the province of distribution of the group of *P. machaon*. A glance at his tables (Pl. vi–viii), however, shows that this is not the case.

‡ See *Grundzüge*, etc., p. 31, and *Amer. Jour. Sci.*, p. 63, et seq., 1896.

This prevention of migration is very important. *Migration* (as understood by M. Wagner) is an accessory factor, often coöperating with separation, and often working against it. Each species, which originated in a limited area, tends to occupy other territories: it is a well-known fact that each animal form possesses its peculiar "means of dispersal," and by such means it migrates. Migrating species occupy new territories, which have either the same or slightly different conditions of life: in the latter case migration by itself may induce new variations in consequence of the slightly modified action of the external conditions of life. Further, migration is often slow, or only possible under peculiar circumstances, often it is accidental, and only a few individuals can transgress the original limits on rare occasions: then even migration acts as a means of separation. The few individuals occupying a new locality are afterwards practically separated from the original stock remaining in their native country, and thus they may develop separately into a different species, even in the case that immigration from the original stock is not altogether impossible, since any rare individuals of the latter, reaching the new colony from time to time, are soon absorbed by the new form and their characters disappear by the continuous crossing with the modified individuals and by the transforming power of the external conditions. Separation, however, is not always connected with migration: the original "centre of origin" of a species may be broken up again into parts, thus inducing the origin of new species, if the external conditions favor it.

Separation in any form may be more or less complete, and since between complete continuity and complete separation intermediate steps are interposed, also a complete differentiation of species is reached by degrees. This corresponds exactly with what we see in nature. We know of many groups, the species of which are very insufficiently limited and pass gradually into each other: in such cases the formation of species is not yet accomplished. It is an incomplete separation, if a species occupying a large area is divided into different varieties, which are locally more or less limited, and differ in most remote localities considerably, while in intermediate places intermediate forms are present. The distinct varieties on the most extreme limits of the range are certainly under different conditions of life, but in the intermediate area transitions are present: a complete differentiation of species is not yet reached here, and we have to regard these forms still as varieties.

Of course, it is possible, that nearly allied species, which originated separately, may occupy by migration the same territory and come into competition with each other. If their morphological and physiological peculiarities are not sufficiently fixed, there may result by hybridization a new species. But if the characters are well fixed by inheritance, especially if there is "kyesamechania," they may live together or the stronger may suppress the weaker. But I may safely say, that it is very improbable that two closely allied species ever lived precisely under the same conditions in the same locality. I refer in this respect to the example of four

species of the Derapod genus *Gelasimus* on the East African coast recorded by me.* These four species lived in a particular locality completely separated, although often only a few yards from each other, and a collector less careful would have put them all together in one jar. Yet as a rule collectors are well acquainted with the fact that particular species are to be sought for in particular localities.

IV. I may, I think, conclude. I have amply demonstrated that only *separation* can effect differentiation of species, and that all the principles created by other authors for this particular effect come under the head of separation, *i. e*, the breaking up of a number of individuals into groups, each subject to particular conditions of life. Some authors, indeed, have not understood at all that the whole process ending in the formation of species is composed of a series of distinct factors, only the last of which is separation. But I wish to say here expressly that already Darwin conceived those different factors correctly, and distinguished them well according to their particular line of action. The only change of Darwin's views that I should like to propose is to substitute for his "principle of divergence" that of "separation." Besides, it would be well to conceive the term "Natural Selection" in a modified sense, as Pfeffer has proposed, and we have seen that there is some advantage in so doing. And farther, Eimer has pointed out that not all the characters of each animal form are subject to natural selection: there are many which do not bear on utility, but are indifferent in this respect. But since such characters are probably also due to the influence of external conditions, they may be transmitted and may increase, giving origin to a distinct direction of variation,† to a "mutation," which is independent of natural selection, and may be called by Eimer's term "Orthogenesis."

For the rest, the whole of Darwin's theory stands, and none of those "Darwinists after Darwin"—I venture to say—have been able to weaken any of his ideas in the least degree. Especially Weismann has not, since

*See *Grundzüge*, etc., p. 33, footnote. Compare also the following sentences of Petersen (*Det Videnskabelige Udbytte af Kanonbaadens Hauchs Togter*, 1893, p. 455): "Each species seems to be distributed according to certain rules, which . . . . can be brought in relation to one or several . . . . natural conditions," and (p. 457): "no species is found everywhere in our seas," and farther: F. Dahl, "Vergleichende Untersuchungen über die Lebensweise wirbelloser Aasfresser," *Sitz. Ber. Akad. Wiss. Berlin*, January, 1896, pp. 29, 30.

†Already Darwin holds the same opinion and concedes (*Origin of Species*, pp. 170, 171), that there are variations which appear to be of no service whatever to their possessors. This passage is the more interesting, since he talks of the "laws of growth," which are apparently identical with Eimer's "Gesetzen organischen Wachsens." Comp. farther, *ibid.*, p. 175: "When from the nature of the organism and of the conditions, modifications have been induced which are unimportant for the welfare of the species, they may be and apparently often have been transmitted . . . . to numerous . . . . descendants," and p. 176: "Morphological differences, which we consider as *unimportant* . . . . first appeared . . . . as fluctuating variations, which sooner or later became constant through the nature of the organism and the surrounding conditions." (In the last passage the word I have italicized stands originally as *important*, but according to the foregoing and following sentences this is no doubt a misprint)

it is now demonstrated by the ablest scientists explicitly,* and by many others incidentally, that his theories are without any proper foundation. As regards Eimer's theories, I have endeavored in the above to show, that the alleged opposition in certain points to Darwin does not exist, except as Eimer creates new scientific terms for old ideas, and as he does not distinguish properly between cause and effect.

To sum up, we have to distinguish *four factors*† accomplishing the diversity, development and differentiation into species of organic beings : we may call conveniently this whole process : *origin of species.*

1. All organic beings *vary.* There exists an "inherent tendency to vary,"‡ but this tendency is manifested only by the influence of external causes upon the respective organism. The faculty of variation is an unlimited one,§ but the actual variation is limited, namely by the external conditions of life. Variations coming into existence are modifications "directly due to the physical conditions of life," which "in this sense are supposed not to be inherited."‖ *A variation is impossible without external conditions producing it.*

2. *These variations may be transmitted to descendants.*¶ Inheritance is due to the process of propagation, which may be either by *one* parent or by *two* parents (Amphimixis). By inheritance acquired characters are transmitted from the parent to the descendants, and thus the consanguinity becomes morphologically visible, and individuals of common descent are more closely connected by morphological characters with each other than with any other group of individuals. By inheritance the unsteady and temporary variations are transformed into *varieties,* that is to say, into groups of individuals having the same ancestors and resembling each other more or less.**

*I refer to the following names: Eimer, Haacke, Haeckel, O. Hertwig, Pfeffer, Romanes, Spencer, and others. I would especially mention O. Hertwig's book, *Zeit- und Streit-Fragen der Biologie*, Heft i, "Praeformation oder Epigenesis." I recommend this masterpiece of criticism for study, not only because it refutes completely Weismann's fantastic germ-plasma theory, but because the exposition of this theory given in that work is much more intelligible than that given by Weismann himself. In his latest paper ("Germinal Selection," pp. 282, 285 and 286) Weismann refers to Hertwig's criticism: but his remarks are entirely aside from the question, since they do not touch the chief point, and, partly (p. 282), attribute to Hertwig an opinion which the latter, according to his own express statement, did not entertain (see pp. 10 and 11 of Hertwig's book).

†See *Grundzüge*, etc., p. 32.

‡Darwin, *Var. and Domes.*, p. 2.

§Unless checked by inheritance!

‖Darwin, *Orig.*, p. 33.

¶The transmission of acquired characters is denied by many competent naturalists and cannot be regarded as demonstrated. In the problems of geographical distribution one is continually brought back to this as a probable assumption, and I propound it here as a "working hypothesis."

**Darwin, *Orig.*, p. 33: In "the term variety . . . . community of descent is . . . . implied."

The process of inheritance is most obscure.* We know nothing of the causes of inheritance or—perhaps it is better to say—of non-inheritance often occurring. Weismann's theory of inheritance, even if we accept it (as I do not), does not explain the essence of heredity: it merely refers inheritance to minute processes in fertilization. But this knowledge that heredity is due to the peculiarities in propagation is a very old one, as old as modern zoölogy and perhaps even older, and more accurate knowledge of the minute details in propagation, and their arbitrary augmentation by supposed complications does not promote our understanding of heredity. Yet we do not know how the "tendencies of inheritance" of the germs (or parts of the germs) are transferred to the "soma" of the descendants; we do not know how the germs get these "tendencies" from the "soma" of the parents; we do not know why certain "tendencies" become visible in the descendants, while others do not; we do not know what a "tendency of inheritance" is like anyhow.† A theory of inheritance has to endeavor to answer the questions put here, otherwise it does not explain anything, and the essence of heredity continues to be as obscure as before.

By inheritance and repeated action of particular external conditions a distinct direction of variation may be induced: certain animal forms tend again and again to vary in the same direction, and the degree of the variations is thus increased. This process is what Eimer calls orthogenesis, and if the action of the external conditions as well as of inheritance is not a steady one, but interrupted and irregular, we have his halmatogenesis. Both terms clearly come under the head of inheritance. Orthogenesis and halmatogenesis can effect "mutations," but we must bear in mind that here no principle of utility comes into play.

It is well to be noted that the two factors mentioned, variation and inheritance, act only upon single individuals. They act often upon a number of individuals in the same or analogous manner, but each individual can vary and inherit without regard to others. The two following principles (natural selection and separation) can only act upon a multitude of individuals simultaneously, and their action becomes conspicuous only by the comparison of many individuals.

3. Upon the material produced by variation and inheritance acts a third factor: *Natural Selection.* By this principle all variations injurious in the struggle for existence, all the forms not fitted for existence under a

*See Osborn ("The Hereditary Mechanism and the Search for the Unknown Factors of Evolution," *Biol. Lect. Mar. Biol. Lab.*, Wood's Holl, 1895): "If acquired variations are transmitted there must be some unknown principle in heredity."

†Of course, Weismann has tried to answer these questions, at least partly, by his "theories," but such questions cannot be explained at all by "theories," the very foundations of which are either disputable or arbitrary, or even illogical and contrary to the known facts. On the whole, Weismann's arguments run in a perfect *circulus vitiosus.* His theory of inheritance is founded upon the belief that acquired variations are not transmitted, and the demonstration, that acquired variations are not transmitted, is founded upon the belief that his theory is correct (comp. *Neue Gedanken zur Vererbungsfrage*, 1895, pp. 11 and 21).

certain sum of conditions of life are destroyed. The remnant left is fit for existence, and all the individuals surviving are able to live and propagate. There may be slight differences between them, especially as regards characters not bearing on utility, but a certain average of good characters is present. Natural selection at least preserves this good average, and if there arise any useful characters, a smaller percentage of the individuals possessing the latter is destroyed, and thus the better individuals may gain little by little the preponderance in number: the average is displaced slowly in a distinct direction, namely, toward the better. This latter "mutation" is distinguished from the mutation by orthogenesis by the advantage connected with the particular line in which the change advances. Natural selection effects a general adaptation of the whole number of the surviving individuals to particular conditions of life.

4. But natural selection does not form species; it only preserves or transforms already existing species. If we suppose, however, that of the individuals surviving in natural selection different groups are *separated* from each other under different conditions, and that this *separation* cannot be overcome, so that each group must remain under the constant action of particular conditions, the difference of the latter effects, that each group tends to develop its characters in a different direction. It is true, if upon each separated group the same external conditions act in the same manner, there would be, of course, no separation of the directions of development. But differentiation of the external conditions by bionomic separation, and the splitting into groups of individuals living formerly under the same conditions will give origin to different characters in each group, and animals distinguished by the constant presence of different characters we call *species*. *Different species are formed by bionomic separation; separation does not always imply differentiation of the conditions of life, and accordingly does not always form new species; but if there is a differentiation into species, it is always due to separation under different bionomic conditions.*

In the above the particular action of each of the four chief factors playing a part in the evolution and diversification of the organic world is properly limited. We have seen that the two last-named factors, selection and separation, are imitated by man in the breeding of domesticated animals. Both nature and man use the material furnished by variation, and the success of both is warranted under the condition that the acquired characters may be fixed by hereditary transmission. The four factors named, *variation*, *inheritance*, *selection* and *separation*, must work together, in order to obtain different species, and, indeed, they do so always; it is impossible to think that one of them should work by itself, or that one could be left aside.

The proper action of each of these factors was recognized almost correctly by Darwin, only as respects the differentiation of species, which he attributes to the principle of divergence, he was not quite satisfied.* But

* Darwin, *Origin*, p. 87: "Though it was a long time before I saw how."

most of the successors of Darwin, especially those who pretended to have modified, corrected or enlarged his views in any respect, have not understood his theory correctly: generally the origin of variations, varieties and species has been hopelessly confused, and the latter is especially true of the writings of Weismann, in which the origin of species and varieties, and the origin of the adaptive characters of life are mixed up constantly.*

In, conclusion I should like to add that the principle of separation, as set forth above, bears very importantly on the definition of the systematic term *Species*, and indeed, that it alone enables us to give a correct definition of it. There is no doubt that a proper and logical definition of any term depends largely on the knowledge of the genesis of the object, and in the present case we may say that if the process of the formation of species is properly understood, we can derive from this knowledge a definition of the term species. In my book often above referred to, I have propounded the following:† "*We designate as* SPECIES *such forms as in consequence of* SEPARATION *differ sharply and constantly by morphological characters from allied coëxisting forms.*" It is not necessary that separation should be still evident in all the existing species: the separating causes have often disappeared, while their result, the different species, still exist. But then the separation in the past must have been sufficient to modify and differentiate the respective forms in such a degree that the characters are fixed by inheritance, so that changed external conditions cannot influence them again, and farther, there must be kyesamechania, which prevents hybridization. The possibility, however, of hybridization by artificial means cannot be always regarded as a proof against the value of the respective forms as species: if two species live separated they do not interbreed in nature, and if they are forced to do so, this possibility cannot affect their value as species under normal and natural conditions.

As separation is reached by degrees, distinct species must have developed gradually, and such must still develop. We know numerous examples of so-called "polymorphous" genera, where apparently the process of formation of species is beginning or not yet accomplished. It is true, variations, varieties, and species pass gradually into each other, but this does not imply that these three terms shall be treated alike, and that there is no difference at all between them. A tree is not a shrub, although there are intermediate growths. So we can give a correct definition of variety and species, although there are intermediate forms, which may be doubted, whether they belong to the one or the other.

* This confusion of Weismann's ideas is most evident in the two last pages of his latest publication ("Germinal Selection," *The Monist*, Vol. 6, No. 2, January, 1896, pp. 292, 293). This whole paper is devoted to the demonstration of the action of natural selection as effecting *adaptation*, and though he says that "the mode of formation of the living world as a whole" may be understood by this principle!

† See *l. c.*, p. 32.

The principle of *constant difference* is practically applied generally by systematists, and I hope I have given above a logical foundation of this principle. In many cases, indeed, the constancy of difference is the only means by which species can be distinguished, if the former or the actual separation of the respective forms cannot be made out with certainty. But in all cases, where an actual separation is evident, we should consider the respective forms, if morphologically distinct, as species, not as varieties. Under the new definition of the term species given here, many of the so-called local varieties become species, since such are often distinguished only because the differences from "good" species are only slight ones and are not considered as important enough to create a distinct species. But this standpoint is not correct: any difference in characters, however slight, constitutes a distinct species, if constant and due to separation.